



Stable oxygen-hydrogen isotopes reveal water use strategies of *Tamarix taklamakanensis* in the Taklimakan Desert, China

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Abstract: *Tamarix taklamakanensis*, a dominant species in the Taklimakan Desert of China, plays a crucial role in stabilizing sand dunes and maintaining regional ecosystem stability. This study aimed to determine the water use strategies of *T. taklamakanensis* in the Taklimakan Desert under a falling groundwater depth. Four typical *T. taklamakanensis* nabkha habitats (sandy desert of Tazhong site, saline desert-alluvial plain of Qiemo site, desert-oasis ecotone of Qira site and desert-oasis ecotone of Aral site) were selected with different climate, soil, groundwater and plant cover conditions. Stable isotope values of hydrogen and oxygen were measured for plant xylem water, soil water (soil depths within 0–500 cm), snowmelt water and groundwater in the different habitats. Four potential water sources for *T. taklamakanensis*, defined as shallow, middle and deep soil water, as well as groundwater, were investigated using a Bayesian isotope mixing model. It was found that groundwater in the Taklimakan Desert was not completely recharged by precipitation, but through the river runoff from snowmelt water in the nearby mountain ranges. The surface soil water content was quickly depleted by strong evaporation, groundwater depth was relatively shallow and the height of *T. taklamakanensis* nabkha was relatively low, thus *T. taklamakanensis* primarily utilized the middle ($23\% \pm 1\%$) and deep ($31\% \pm 5\%$) soil water and groundwater ($36\% \pm 2\%$) within the sandy desert habitat. *T. taklamakanensis* mainly used the deep soil water ($55\% \pm 4\%$) and a small amount of groundwater ($25\% \pm 2\%$) within the saline desert-alluvial plain habitat, where the soil water content was relatively high and the groundwater depth was shallow. In contrast, within the desert-oasis ecotone in the Qira and Aral sites, *T. taklamakanensis* primarily utilized the deep soil water ($35\% \pm 1\%$ and $38\% \pm 2\%$, respectively) and may also use groundwater because the height of *T. taklamakanensis* nabkha was relatively high in these habitats and the soil water content was relatively low, which is associated with the reduced groundwater depth due to excessive water resource exploitation and utilization by surrounding cities. Consequently, *T. taklamakanensis* showed distinct water use strategies among the different habitats and primarily depended on the relatively stable water sources (deep soil water and groundwater), reflecting its adaptations to the different habitats in the arid desert environment. These findings improve our understanding on determining the water sources and water use strategies of *T. taklamakanensis* in the Taklimakan Desert.

Keywords: *Tamarix taklamakanensis*; water use strategies; stable isotopes; Bayesian isotope mixing model; deep soil water; groundwater; Taklimakan Desert

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1 Introduction

Water is an indispensable factor for plant growth, vegetation distribution and community composition (Rosenthal et al., 2005; Zhou et al., 2013; Zhang et al., 2018). In the desert ecosystem, water is extraordinarily valuable and has a decisive impact on the survival and distribution of plants. In addition, precipitation and groundwater are the primary water sources in the desert ecosystem and groundwater plays a vital role in shaping plant adaptations because precipitation is very limited and unpredictable (Dai et al., 2015). In the past decades, it was commonly accepted that soil moisture was the remains of the last precipitation event in the desert environment (Evaristo et al., 2016). However, previous studies have indicated that in shifting sand dunes, rainfall of <13.40 mm cannot be utilized by plants as it may be completely evaporated before infiltrating into the deep soil layer (Chen et al., 2003; Liu et al., 2006). Furthermore, soil water content (SWC) in the desert ecosystem is extremely variable in both space and time (Zhou et al., 2017). Therefore, desert plants are generally under chronic or periodic water-deficit conditions. Perennial plants have to adjust their water use strategies to survive and meet their growth and metabolism requirements, and their roots must acquire sufficient groundwater or residual soil water to tolerate prolonged drought (Tiemuerbieke et al., 2018). Likewise, desert plants are accompanied by high vulnerability to climatic change in the extreme habitats. Moreover, climate change and over-exploitation of groundwater could severely injure desert species and affect the frail ecosystem (Dai et al., 2015; Zhang et al., 2018). Therefore, it is critical to obtain a high level of comprehension about the water use strategies of plants in the desert environment.

The Taklimakan Desert is the largest shifting sand desert in China. Sand dunes throughout the desert were formed in alignment by aeolian sand. The desert has been severely affected by human activities and is, thus, highly susceptible to changes in water availability. As the dominant species in this desert, *Tamarix taklamakanensis* plays a crucial role in stabilizing sand dunes and maintaining the function and structure of the desert ecosystem (Zhao et al., 2011). In the Taklimakan Desert, a long-term accumulation of the alternate sand layers and litter layers around *T. taklamakanensis* (Muhtar et al., 2002; Xia et al., 2004) results in the formation of a specific biogeographic unit called the *T. taklamakanensis* nabkha, with the heights ranging from 3 to 15 m and lengths from 5 to 50 m (long axis) (Zhao et al., 2011). *T. taklamakanensis* nabkha is mainly distributed in the lower reaches of the Tarim River and the hinterland of the Taklimakan Desert (Zhao and Xia, 2011). However, degeneration and extinction of *T. taklamakanensis* nabkha have occurred in the desert ecosystem as a result of human activities and climate change, and this may directly affect the stability of the local desert ecosystem (Zhao and Xia, 2011). Currently, little is known about the water use strategies of *T. taklamakanensis* at the *T. taklamakanensis* nabkha locations in the desert ecosystem. A clear understanding of the water sources used by *T. taklamakanensis* will help us to assess the effects of human activities and climate change on the local ecosystem.

Stable isotope analysis is a powerful tool that has been extensively utilized to identify the water sources of plants (Schachtschneider and February, 2010; Dai et al., 2015; Evaristo et al., 2016; Zhou et al., 2017; Tiemuerbieke et al., 2018). Due to the influences of physical and climatic factors, different water sources in nature have diverse isotope signatures (Craig, 1961; Schachtschneider and February, 2010; Tiemuerbieke et al., 2018), and the stable isotope fractionation is not generally observed in the water uptake processes of root systems from soils (Evaristo et al., 2016). Thus, the stable isotope information of potential water sources can be reflected by the isotope composition of plant xylem water (Si et al., 2014; Tiemuerbieke et al., 2018). Plant water sources can be identified by comparing the isotope ratios of plant xylem water to the isotope concentrations of all potential water sources (Dai et al., 2015; Wu et al., 2016; Tiemuerbieke et al., 2018). In China, the water sources and water use strategies of *Tamarix ramosissima*, *Tamarix laxa* and *Tamarix chinensis* have previously been explored in the Gurbantunggut Desert, Badain Jaran Desert, Heihe River Basin and Dunhuang Oasis by many researchers (Cui et al., 2015; Sun et al., 2016; Wu et al., 2016; Zhang et al., 2018), and their findings indicated that the growth of these plants relies on water sources from

different soil depths (Wu et al., 2014; Cui et al., 2015; Zhang et al., 2018). However, previous studies on water use of *T. ramosissima* have mainly focused on the desert riparian belt, and the upper and lower reaches of the Tarim River Basin (Wang et al., 2017; Zhou et al., 2017). Some studies have observed that *T. ramosissima* primarily used groundwater in the Tarim River Basin, and also utilized deep soil water below 200 cm (Li et al., 2009; Zhao and Xia, 2011). Nevertheless, because of the influences of environmental factors (e.g., precipitation, groundwater depth and micro-topography) and human activities in the different habitats of *T. taklamakanensis*, the understanding of potential water sources and water use strategies of *T. taklamakanensis* is severely limited. This is particularly the case in the desert environment, where the water use strategies of *T. taklamakanensis* within the *T. taklamakanensis* nabkha represent a critical research gap, even though the habitats of *T. taklamakanensis* are crucial in our comprehending of the chronically adaptive mechanisms of desert plants to the spatial pattern change of soil water.

The aim of our study was to determine the water sources and water use strategies of *T. taklamakanensis* in four habitats (sandy desert of Tazhong, saline desert-alluvial plain of Qiemo, desert-oasis ecotone of Qira and desert-oasis ecotone of Aral) in the center and fringe of the Taklimakan Desert, using the stable isotope approach. Given the known differences in micro-climate, soil and groundwater depth in the different habitats (Zhao and Xia, 2011; Zeng and Song, 2013), our first hypothesis was that *T. taklamakanensis* has different water use strategies within different habitats. Likewise, considering that aridity is a typical feature in the Taklimakan Desert and plant roots in the surface soil layer may be inactive because of the long-lasting periods of low SWC, our second hypothesis was that this species mainly utilizes middle and deep soil water and/or groundwater, especially for the habitats with extremely arid climate conditions.

2 Materials and methods

2.1 Study sites

The Taklimakan Desert is located in Northwest China and covers an area of 33.76×10^4 km² (37°–41°N, 77°–90°E), with approximately 85% of its environment composed of shifting sand (Sun and Liu, 2006). It is known to be a significant sand-dust source area with the frequency of dust events being up to 100 d/a (Wang et al., 2005). The mean annual precipitation ranges from 24.00 to 65.30 mm and the mean annual evaporation extends up to 3000.00 mm, which is about 30–140 times larger than the amount of precipitation. Precipitation occurring in summer quickly evaporates from the surface soil layers under high evaporation, resulting in decreased surface soil water. Tributaries and transitional rivers, formed by the snowmelt water from the mountains over the summer, permit the formation of oases along the desert fringe (Bruehlheide et al., 2003). Since there is no rainy season, typically no annual plants grow in this region. The predominant species are mainly shrubs, including *T. taklamakanensis*, *Populus euphratica*, *Karelinia caspia* and *Alhagi sparsifolia*.

The formation and development of *T. taklamakanensis* nabkha are mainly affected by wind erosion and hydraulic erosion. Four sampling sites with different micro-climates, soil types and vegetation cover conditions were selected to cover the typical range of *T. taklamakanensis* nabkha habitats within the Taklimakan Desert (Fig. 1; Table 1; Dong et al., 2018). Sampling site A was located in the central Taklimakan Desert, near the Taklimakan Desert Research Station of Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences. The plant cover of *T. taklamakanensis* nabkha was approximately 20% and the surface of *T. taklamakanensis* nabkha was characterized by scattered shifting sand. Sampling site B was located near the Qiemo County in the southeastern fringe of the Taklimakan Desert along the desert highway, which is the transition zone between alluvial plain and desert. The plant cover of *T. taklamakanensis* nabkha was 50% and the saline soil and strong evaporation in summer had contributed to the formation of salt crust on the soil surface. Sampling site C was situated in the southern fringe of the Taklimakan Desert, with the distance of about 10 km from the Qira County. This region is a desert-oasis ecotone. The plant cover of *T. taklamakanensis* nabkha was 30%–35% and the soil surface was dominated by shifting sand with light salinization. Sampling site D was located near the city of Aral in the northern fringe of the

Taklimakan Desert. This region is also a desert-oasis ecotone. The plant cover of *T. taklamakanensis* nabkha was 40%–45% and the soil surface was moderately salinized and covered by a thin salt crust (Table 1). In the four sampling sites, the soil was mainly aeolian sand in texture.

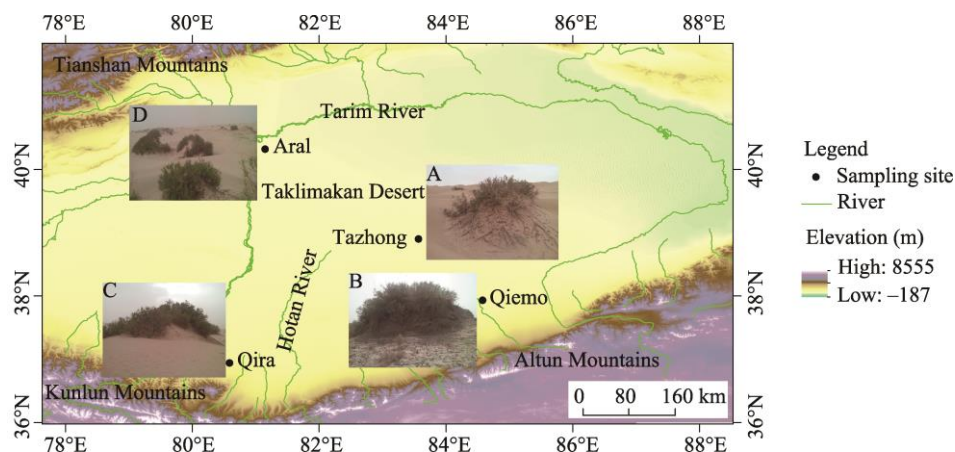


Fig. 1 Location of sampling sites in the Taklimakan Desert. A, B, C and D represent the four sampling sites of *Tamarix taklamakanensis* habitats. A, sandy desert of Tazhong site; B, saline desert-alluvial plain of Qiemo site; C, desert-oasis ecotone of Qira site; D, desert-oasis ecotone of Aral site. It should be noted that only the important rivers are marked in the figure.

At each sampling site, four mature individual *T. taklamakanensis* nabkhas were selected, and the adjacent sampling nabkhas (about 500 m apart) were considered representative of middle-sized nabkha. At all the sampling sites, the average height, length and width of *T. taklamakanensis* nabkhas were $3.13 (\pm 0.53)$, $7.37 (\pm 0.66)$ and $5.72 (\pm 0.46)$ m, respectively (Table 1).

Table 1 Meteorological and habitat data of the sampling sites within the Taklimakan Desert

Site	Location	Groundwater depth (m)	Soil surface	<i>Tamarix taklamakanensis</i> nabkha				AMT (°C)	MAP (mm)	MAEP (mm)
				Plant cover (%)	Height (m)	Length (m)	Width (m)			
Tazhong	39.06°N	5.0–6.0	Aeolian sandy soil	20	2.64	6.71	5.37	11.82	25.11	3559.60
	83.67°E									
Qiemo	38.03°N	4.5–5.5	Salt crust and aeolian sandy soil	50	3.27	7.45	5.89	10.68	27.97	2360.60
	84.68°E									
Qira	37.04°N	11.0–16.0	Shifting sand with light salinization	30–35	3.53	7.87	6.10	12.52	41.67	2790.20
	80.69°E									
Aral	40.42°N	8.0–10.0	Slight crust and moderately salinization	40–45	3.08	7.23	5.59	10.97	51.54	1813.20
	81.25°E									

Note: AMT, annual mean temperature; MAP, mean annual precipitation; MAEP, mean annual evaporation. The climatic data are referred from Gong et al. (2011), Fan et al. (2013), and Zeng and Song (2013).

2.2 Sample collection and analysis

Field sampling was conducted in July 2017. It should be noted that no precipitation events occurred during the sampling period. In general, the material was sampled at mid-day. In each sampling site, four soil cores were collected from the four *T. taklamakanensis* nabkhas using a handheld auger. Finally, a total of 16 soil cores were sampled at each sampling site. Based on our prior knowledge of soil water isotope along the soil profile (Zhao and Xia, 2011), we collected soil samples within the 0–500 cm depth at an interval of 20 cm. Each soil sample was separated into two subsamples: one subsample was packaged immediately in an airtight bottle and refrigerated at -20°C until isotope analysis, and the other subsample was sealed in soil tins for SWC analysis by the oven-drying method. Soil particle size fractions were measured using a laser particle sizer (Mastersizer 2000, Malvern Instruments Ltd., Worcestershire, UK). According to the US classification standards, we classified the soil particle size into four types: clay (<0.002 mm), silt (0.002–0.050 mm), very fine

sand (0.050–0.100 mm) and fine sand (0.100–0.250 mm).

Plant samples were collected on the same days as the soil sample collection. Six twigs of *T. taklamakanensis* were sampled from each *T. taklamakanensis* nabkha. To avoid isotope fractionation of plant xylem water, we sampled the completely suberized twigs (diameter: 0.3–0.5 cm; length: 4.0–5.0 cm) for the extraction of plant xylem water. As soon as sampling, the green tissues, including all leaves and green bark, were removed quickly from the stems. Then, all plant samples were promptly put into the screw-cap glass bottles, sealed with parafilm and stored in a freezer (−20°C) until isotope analysis.

Groundwater samples were obtained from the nearby wells approximately 10–20 km from each site. To reflect the potential contribution of snowmelt water to the groundwater isotope signature, we collected snowmelt water from bedrock canyon in the Tianshan Mountains and Kunlun Mountains. Snowmelt water is representative of the perennial precipitation in the Taklimakan Desert. Both groundwater and snowmelt water samples were rapidly put into glass vials and sealed with parafilm and stored in a fridge at 4°C for later isotope analysis.

2.3 Stable isotope analysis

We used deuterium (^2H) and oxygen (^{18}O) isotope values of soil water and groundwater to describe the potential water sources, which were compared with the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of plant xylem water. Soil water and plant xylem water were extracted using a cryogenic vacuum distillation apparatus (PicarroL2120-I, USA) (Evaristo et al., 2016). Plant xylem water, soil water, groundwater and snowmelt water samples were filtered using 0.22- μm pore size filters and each sample was pipetted into a small screw-cap glass vial, sealed with parafilm and refrigerated at 2°C.

The liquid water isotope analyzer (DLT-100, Los Gatos Research Inc., Mountain View, USA) was utilized for stable isotope measurements. The analytical precision of individual measurements was $\pm 0.25\text{‰}$ and $\pm 1.00\text{‰}$ for $\delta^{18}\text{O}$ and $\delta^2\text{H}$, respectively. The stable isotope values can be expressed as:

$$\delta(^2\text{H}, ^{18}\text{O})(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\text{‰}, \quad (1)$$

where R_{sample} and R_{standard} are the stable isotope values (molar ratios of $^2\text{H}:\text{H}$ and $^{18}\text{O}:^{16}\text{O}$) of the sample and the standard water (standard mean ocean water), respectively (Dawson et al., 2002). Given the low water content, the stable isotope values of plant xylem water and soil water may be erroneous because of the organic contamination from methanol and ethanol. Thus, to eliminate the spectral contamination, we corrected the stable isotope values of plant xylem water and soil water by a standard curve (Schultz et al., 2011).

2.4 Classification of water sources

A Bayesian isotope mixing model was used for the identification of plant water sources in the different habitats. The Bayesian isotope mixing model takes into account both $\delta^{18}\text{O}$ and $\delta^2\text{H}$ and the results are generally more robust. This model utilizes the Bayesian framework to identify the proportional contribution of each source to a mixture. The Bayesian isotope mixing model has been implemented in the software package SIAR (Stable Isotope Analysis in R) (Parnell et al., 2010), which was applied to determine the potential water sources that may contribute to plant xylem water.

Based on the similarities in the $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values of soil water and the SWC within each soil depth in addition to the $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values of plant xylem water, we classified the four potential sources of plant xylem water when running the Bayesian isotope mixing model. The $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values for each soil depth were determined by the SWC-weighted mean approach (Wu et al., 2016) and soil water was categorized as follows: (1) shallow soil water (0–200 cm), which was the most unstable and $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values varied significantly with depths; (2) middle soil water (200–400 cm), which had lower $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values with relatively weak changes; (3) deep soil water (400–500 cm), which had relatively consistent isotope composition and SWC with no significant differences among depths; and (4) groundwater, which had relatively constant $\delta^{18}\text{O}$ and $\delta^2\text{H}$ values.

2.5 Data analysis

Meteorological data were obtained from the Meteorological Information Center of Xinjiang and China Meteorological Data Network (<http://data.cma.cn/data/weatherB-k.html>). All statistical analyses were performed using SAS 9.2 (North Carolina, USA). Tukey's test (t -test) was used to evaluate the differences in isotope compositions of soil water, groundwater and plant xylem water obtained from each sampling site ($P < 0.05$). The relationships between $\delta^{18}\text{O}$ and $\delta^2\text{H}$ were established by using a linear regression model. Figures were plotted using the software Origin 2017 (OriginLab Corp., Northampton, USA).

3 Results and discussion

3.1 Climate characteristics of the sampling sites

The monthly mean temperature was typically lowest in January and highest in July for all sampling sites (Fig. 2). The precipitation mainly occurred between May and August, with approximately 80%–90% of the annual totals in the Tazhong, Qiemo and Qira sites. Approximately 90% of the annual precipitation occurred from May to October in the Aral site. Mean annual evaporation was highest in the Tazhong site, followed by Qira site, while Qiemo and Aral sites had relatively low amounts of evaporation. In the Tazhong site, the plant cover was very low due to the limited precipitation and intensive evaporation (Li et al., 2015). Nevertheless, in the Qira and Aral sites, precipitation was relatively high and evaporation was relatively low compared to the other two sites, and thus the plant cover was relatively high (Table 1). In the Qiemo site, precipitation was very low and the plant cover was relatively high. Plants such as *Phragmites australis* and *Halostachys caspica* were also observed in this site, which may be related to the flood alluvium in summer.

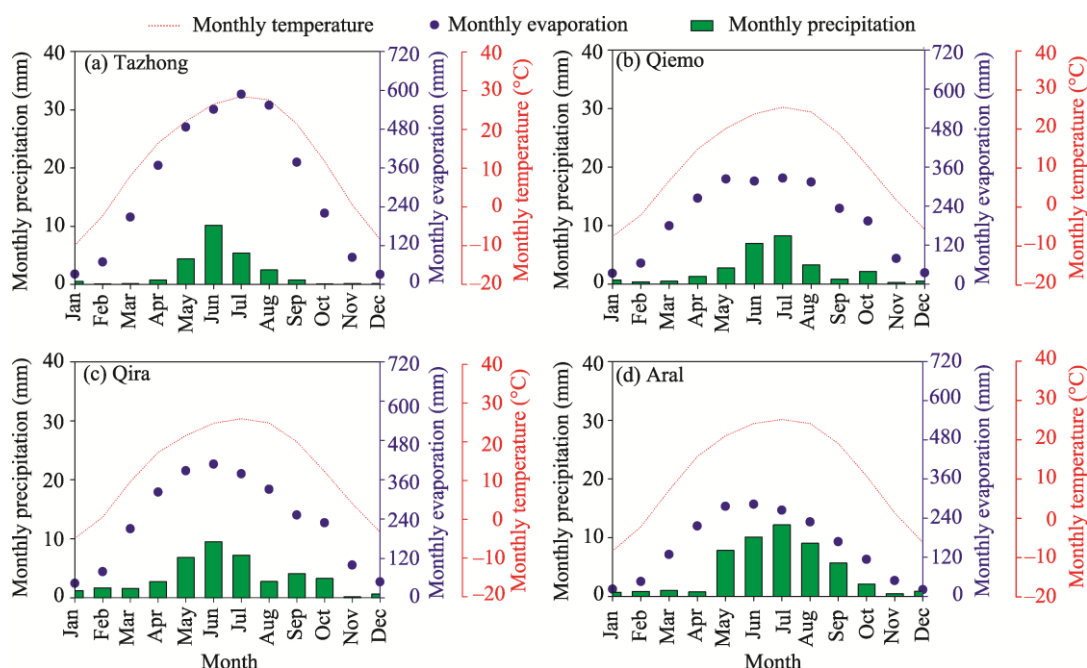


Fig. 2 Monthly precipitation, evaporation and air temperature in the Tazhong (a), Qiemo (b), Qira (c) and Aral (d) sites. The values represent monthly means during 1997–2015 in the Tazhong site and during 1965–2015 in the Qiemo, Qira and Aral sites.

3.2 SWC and stable isotope values of soil water

In the extremely dry desert ecosystem, the SWC is very low and water movement is affected by climate factors, soil properties and groundwater (Li et al., 2010). Previous studies have indicated that rainfall of around 15.00 mm may be entirely evaporated by about 20 d after the rainfall event under

arid climate conditions, therefore infiltrated water cannot be completely enclosed by the sand layer and stored in soil for a long term (Liu et al., 2006; Li et al., 2010). In our study sites, the monthly precipitation was less than 12.00 mm (Fig. 2), and a single precipitation event seldom exceeded 10.00 mm, indicating that the SWC was not fully derived from the precipitation (Si et al., 2014). Thus, we suggest that the influence of precipitation on the SWC is very small in the study sites. The soil in the *T. taklamakanensis* nabkhas was mainly composed of silt and sand (Fig. 3), and this kind of soil texture may be beneficial for a single large amount of rainfall to rapidly infiltrate into the soil and to replenish deep soil water in the Taklimakan Desert. Therefore, the SWC was affected by the factors such as soil texture and groundwater (Figs. 3 and 4a; Si et al., 2014; Cui et al., 2015).

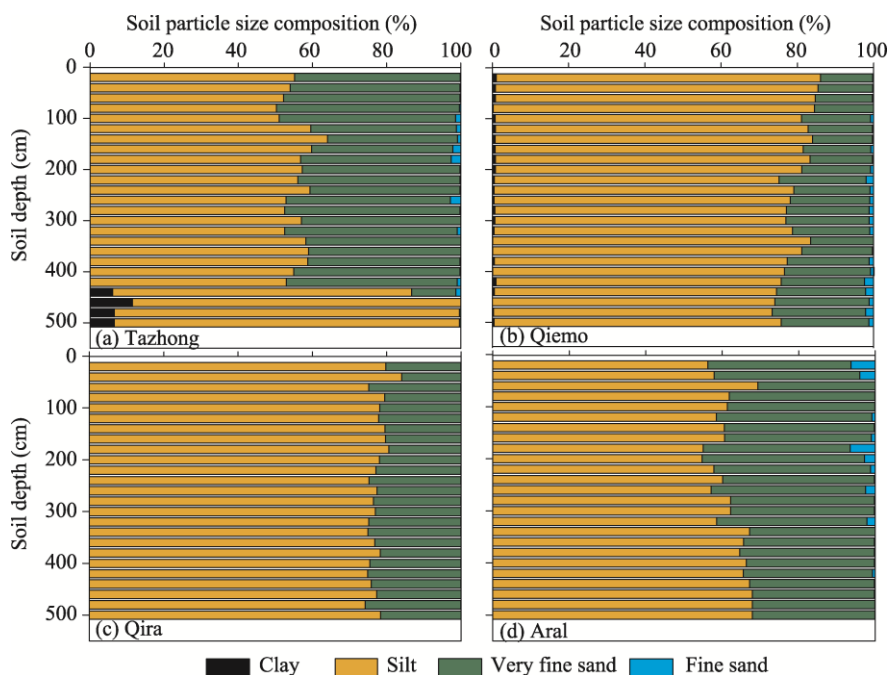


Fig. 3 Vertical distributions of soil particle size composition for the *T. taklamakanensis* nabkhas in the Tazhong (a), Qiemo (b), Qira (c) and Aral (d) sampling sites. Soil particle size composition was described in terms of the percentages of clay (<0.002 mm), silt (0.002–0.050 mm), very fine sand (0.050–0.100 mm) and fine sand (0.100–0.250 mm).

The SWC increased with soil depth for the *T. taklamakanensis* nabkhas in all sampling sites (Fig. 4a). In the Tazhong site, the SWC values within the 0–400 cm soil depth were extremely low, which could be attributed primarily to the sparse precipitation and strong evaporation within this region (Fig. 2). In the Qiemo site, the SWC values within the 0–400 cm soil depth were significantly lower than those within the 400–500 cm soil depth ($P < 0.05$). In addition, the plant cover was as high as 50% in the *T. taklamakanensis* nabkhas and the soil surface has a salt crust, resulting in the SWC significantly higher in the Qiemo site than in the other three sites ($P < 0.05$). Besides, in the 0–400 cm soil depth, the clay content in the Qiemo site was significantly higher than those in the other three sites ($P < 0.05$), which can be attributed to the relatively good water retention capabilities in the Qiemo site (Figs. 3 and 4a). In the Qira site, the upper soil layer (0–200 cm) was affected by strong evaporation, resulting in the low SWC values. The SWC values within the 200–400 cm soil depth exhibited no significant differences in the 400–500 cm soil depth ($P > 0.05$). In the Aral site, the SWC values showed no significant variations within the 0–500 cm soil depth ($P > 0.05$) and were significantly different from those in the other three sites.

Previous studies have demonstrated the enrichment of the heavy isotopes in the shallow soil water relative to the deep soil water and groundwater because of soil surface evaporation (Gat et al., 2007; Zhang et al., 2018). It should be noted that soil water was not extracted from the 0–80 cm soil depth in the Tazhong site and from the 0–20 cm soil depth in the Aral site due to the extreme low SWC in

these soil layers. In the four study sites, evaporation most likely caused the enrichment of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in the shallow soil water (0–200 cm depth; Figs. 4b and c). With increased soil depth, the influence of evaporation would be reduced. The isotope values of soil water in the 200–400 cm soil depth displayed relatively weak variations, and the values below the 400 cm soil depth showed no significant variations in each sampling site (Figs. 4b and c). Accordingly, with increased soil depth, the isotope value decreased gradually to a relatively constant value in all sampling sites, indicating that evaporation had little or no impact on the soil water within the deep soil layers.

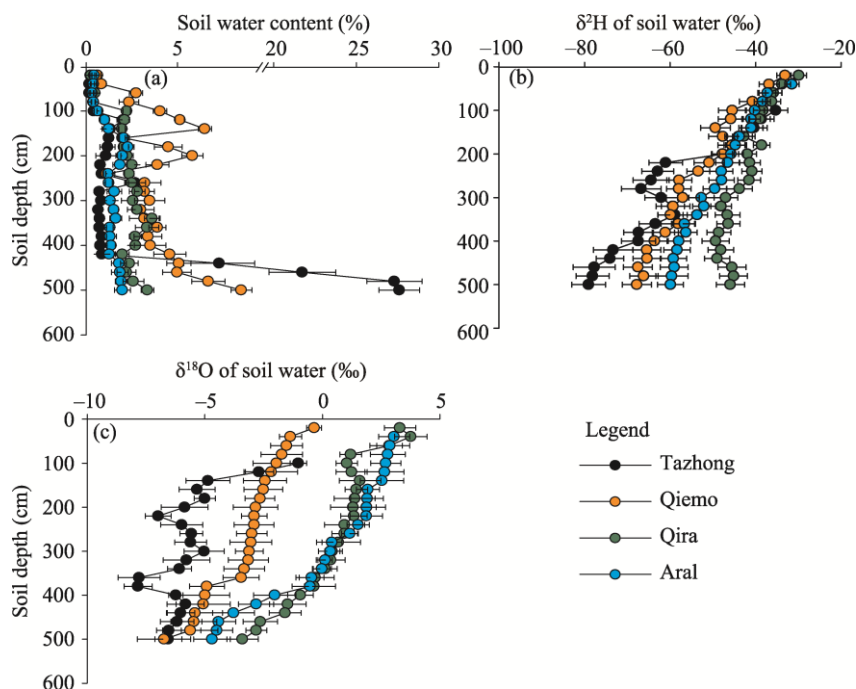


Fig. 4 Vertical distributions of soil water content (a), $\delta^2\text{H}$ (b) and $\delta^{18}\text{O}$ (c) values of soil water within the *T. taklamakanensis* nabkhas in the Tazhong, Qiemo, Qira and Aral sampling sites ($n=4$). Bars mean standard errors.

In the Taklimakan Desert, the mean annual precipitation was very low, so the influences of precipitation on the shallow soil water and the stable isotope ratios of soil water were very small (Liu et al., 2006; Si et al., 2014). In the Tazhong and Qiemo sites, the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ of soil water within the 0–200 cm soil depth were more enriched than those within the 200–500 cm soil depth ($P<0.05$). In addition, the isotope values of soil water in the Tazhong and Qiemo sites were more depleted (especially in the deep soil layers) than the values in the Qira and Aral sites (Figs. 4b and c). The isotope values of soil water decreased with soil depth, and the isotope values of deep soil water similar to the values of groundwater in the Tazhong and Qiemo sites (Figs. 4 and 5), which demonstrated that soil water was recharged by groundwater. In the Qira and Aral sites, the groundwater depth may have declined due to the excessive exploitation and utilization of water resources in populated areas (Fan et al., 2013; Zeng et al., 2013). The $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of soil water within the 0–500 cm soil depth showed significant variations ($P<0.05$). Specifically, the $\delta^{18}\text{O}$ values of soil water were more enriched within the 0–200 cm soil depth than within the 200–400 cm soil depth, and the values were progressively decreased and reached the relative minimum within the 400–500 cm soil depth (Fig. 4c). In addition, the $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of soil water deviated to the right of the $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of groundwater (Figs. 5c and d). Therefore, there was no indication that soil water was recharged by groundwater in the soil depth above 500 cm in the Qira and Aral sites, inferring that the variations in stable isotope values of soil water were affected by evaporation and groundwater depth in these sites.

3.3 Stable isotope ratios of groundwater and possible groundwater recharge sources

The global meteoric water line (GMWL: $\delta^2\text{H}=8\delta^{18}\text{O}+10$; Craig, 1961), the local meteoric water line (LMWL: $\delta^2\text{H}=7.27\delta^{18}\text{O}+6.47$, $R^2=0.94$; Zhou et al., 2017), and the $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of soil water, snowmelt water, groundwater and plant xylem water were plotted in Figure 5.

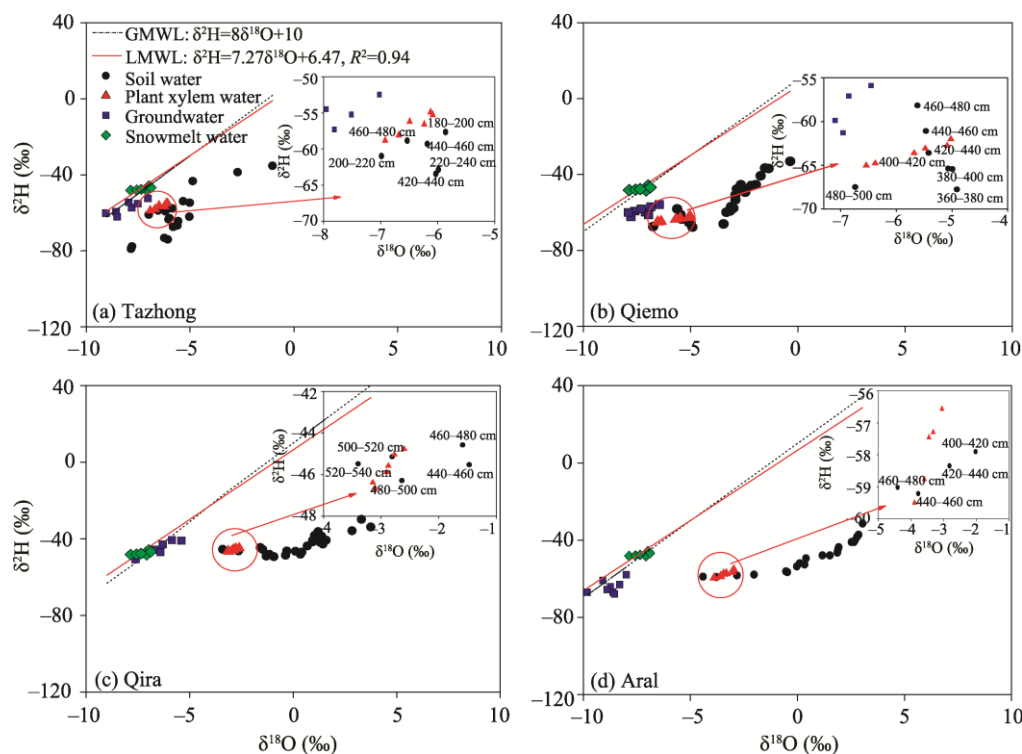


Fig. 5 Relationships between $\delta^2\text{H}$ and $\delta^{18}\text{O}$ in snowmelt water ($n=6$), soil water ($n=4$), groundwater ($n=6$) and plant xylem water ($n=6$) within the *T. taklamakanensis* nabkhas in the Tazhong (a), Qiemo (b), Qira (c) and Aral (d) sampling sites. All samples were taken during the rainless periods. Values of groundwater and snowmelt water represented long-term averages for each sampling site.

The $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of snowmelt water were well matched with the LMWL, which indicated that a proportion of the precipitation was primarily contributed by the local snowmelt water (Fig. 5). The $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of groundwater deviated to the right of the GMWL and LMWL in the Qiemo site (Fig. 5b). The $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of groundwater samples were lower than those of snowmelt water samples (Fig. 5b), but the $\delta^{18}\text{O}$ values of groundwater were similar to those of snowmelt water (Table 2). Nevertheless, the $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of groundwater were close to the GMWL and LMWL in the Tazhong, Qira and Aral sites, but the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of groundwater were higher than those of snowmelt water in the Tazhong and Aral sites (Figs. 5a, c and d; Table 2). This suggests that groundwater can be recharged by snowmelt water runoff.

Ehleringer and Dawson (1992) previously showed that the isotope composition of groundwater was a weighted average of long-term rainfall inputs. Moreover, Mathieu and Bariac (1996) indicated that the recharge processes of groundwater could be divided into two segments: (1) slow infiltration through the soil matrix and the weathered basement; and (2) fast and direct recharge through conducting fissured zones. In this study, we found that the above theory was not completely suitable for the Taklimakan Desert because the mean annual precipitation was very low in this region (Fig. 2) and the rainfall is often totally evaporated before infiltrating into the soil. Therefore, the infrequent precipitation almost exhibits no effect on the growth of plants, and the direct recharge of groundwater by precipitation is probably uncommon. However, groundwater can be also recharged by river runoff from precipitation in nearby mountains in this region (Liu et al., 2012).

3.4 Stable isotope ratios of plant xylem water and possible sources contributing to plant xylem water

The $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of soil water and plant xylem water deviated to the right of the GMWL and LMWL in all sampling sites (Fig. 5). This deviation indicated that plant xylem water and soil water were affected by strong evaporation due to the extremely dry climate conditions. The $\delta^{18}\text{O}$ values of plant xylem water were more depleted in the Tazhong and Qiemo sites than in the Qira and Aral sites. However, the $\delta^2\text{H}$ values of plant xylem water were more depleted in the Qiemo site than in the other three sites. In the Tazhong, Qiemo and Qira sites, the $\delta^2\text{H}$ values of plant xylem water were similar to those of groundwater, and the $\delta^{18}\text{O}$ values of plant xylem water were more enriched than those of groundwater in all sampling sites. The $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of plant xylem water in the Aral site were more enriched than those of groundwater (Table 2). In addition, Cleverly et al. (2002) indicated that the SWC in the surface soil layer was reduced to low levels, and may become inaccessible to the plants under the extremely dry climate conditions. In our study, the $\delta^2\text{H}$ and $\delta^{18}\text{O}$ values of plant xylem water were significantly more depleted than those of soil water within the shallow soil depth. Furthermore, the SWC was very low within the shallow soil depth (0–200 cm) in all sampling sites (Fig. 4). The low SWC were scarcely accessible to *T. taklamakanensis* and enriched isotope values of shallow soil water were little observed within the plant xylem water.

Table 2 Stable isotope ratios of plant xylem water, groundwater and snowmelt water

Site	Plant xylem water		Groundwater		Snowmelt water	
	$\delta^2\text{H}$ (‰)	$\delta^{18}\text{O}$ (‰)	$\delta^2\text{H}$ (‰)	$\delta^{18}\text{O}$ (‰)	$\delta^2\text{H}$ (‰)	$\delta^{18}\text{O}$ (‰)
Tazhong	−56.648 (0.631)	−6.424 (0.136)	−57.332 (1.308)	−8.060 (0.261)		
Qiemo	−63.547 (0.478)	−5.697 (0.261)	−59.232 (0.749)	−7.242 (0.176)	−47.463 (0.407)	−7.285 (0.155)
Qira	−45.718 (0.304)	−2.899 (0.083)	−37.042 (0.929)	−6.472 (0.243)		
Aral	−57.493 (0.608)	−3.378 (0.141)	−64.188 (1.202)	−8.745 (0.194)		

Note: Values in the brackets indicate standard errors.

In this study, field sampling was conducted during the summer (July), the precipitation was judged to be non-significant for plant growth because of the extremely rare precipitation in summer (Chen et al., 2003), and typically no water was found to be stored within the surface soil layer (Fig. 2; Thomas et al., 2008). The potential sources of plant xylem water were identified by employing a Bayesian isotope mixing model, and the results are shown in Figure 6. Furthermore, the probability density graphs for each end-member were also indicated, which were superimposed on the graphs of their relative contributions to plant xylem water. Yakir and Yechieli (1995) showed that plants may differentially utilize water from the soil water of different depths. The use of potential water sources may be an adaptive selection by desert plants to improve their survival under the extremely dry climate conditions (Tiemuerbieke et al., 2018). Therefore, plant xylem water is likely to represent a mixture of different water sources.

T. taklamakanensis indicated a shift in water use strategy among the different habitats. In the Tazhong site, the $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of plant xylem water were similar to the values of soil water in the soil depths of 180–240 cm and below 420 cm and in the layer of groundwater (Fig. 5a). Furthermore, the contributions of shallow, middle and deep soil water and groundwater to the xylem water of *T. taklamakanensis* plants were 10% ($\pm 2\%$), 23% ($\pm 1\%$), 31% ($\pm 5\%$) and 36% ($\pm 2\%$) in this site, respectively (Fig. 6). These results indicated that *T. taklamakanensis*, growing in the sandy desert habitat, had water sources that originated from the multi-layer soil water and groundwater. Nevertheless, due to the extremely rare precipitation and very strong evaporation (Fig. 2), the plant cover in the *T. taklamakanensis* nabkha was very low, the SWC within the shallow and middle soil layers was extremely low ($< 1\%$; Fig. 4), and thus the plants cannot utilize the soil water from the shallow soil layer. The groundwater depth was relatively shallow (5.0–6.0 m) in the Tazhong site (Table 1). Groundwater can recharge the deep soil water due to capillary action (Zhao et al., 2010). Furthermore, we also found that *T. taklamakanensis* had a developed absorption root

system below the 200 cm soil depth, and the root system can even extend the soil depth of below 500 cm (Fig. 7). Therefore, we inferred that middle and deep soil water and groundwater were the primary water sources of xylem water of *T. taklamakanensis* plants in the Taklimakan Desert.

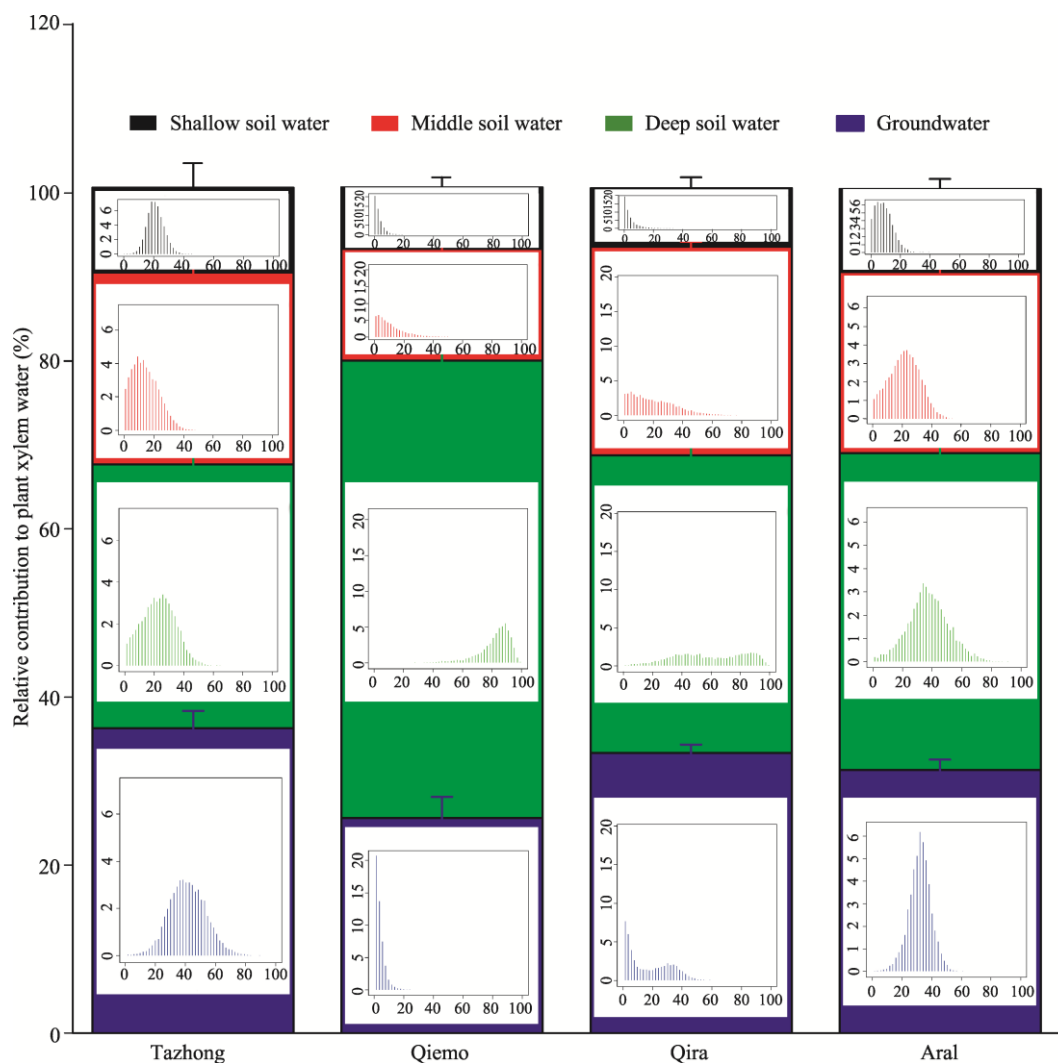


Fig. 6 Relative contributions of shallow, middle and deep soil water and groundwater to the xylem water of *T. taklamakanensis* plants based on the Bayesian isotope mixing model. The respective probability density proportion plots of each possible water source (where the x axis represents the contribution of each possible water source to plant xylem water (%) and the y axis represents the frequency (%)) are superimposed on the plots of relative contributions of different water sources to the xylem water of *T. taklamakanensis* plants. Error bars represent standard errors. The patches of black, red, green and blue represent the relative contributions of shallow soil water, middle soil water, deep soil water and groundwater to the xylem water of *T. taklamakanensis* plants, respectively.

In the Qiemo site, *T. taklamakanensis* nabkhas were mainly distributed in the transition zone between the alluvial plain and the desert. The $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of plant xylem water were similar to the values observed for groundwater and soil water below the soil depth of 360 cm (Fig. 5b). The contribution of deep soil water to the xylem water of *T. taklamakanensis* plants was 55% ($\pm 4\%$), and the contributions of shallow and middle soil water and groundwater were 7% ($\pm 1\%$), 13% ($\pm 1\%$) and 25% ($\pm 2\%$), respectively (Fig. 6). This suggested that plant xylem water was mainly derived from the deep soil water and following the groundwater. Additionally, in the Qiemo site, the surface soil layer had thick salt crusts due to the flood alluvium and evaporation in summer and the groundwater depth was shallow (4.5–5.5 m), resulting in the SWC was relatively high and the plant cover was

also relatively high (50%). These findings further confirmed that *T. taklamakanensis* mainly used the deep soil water and groundwater in this saline desert-alluvial plain habitat.

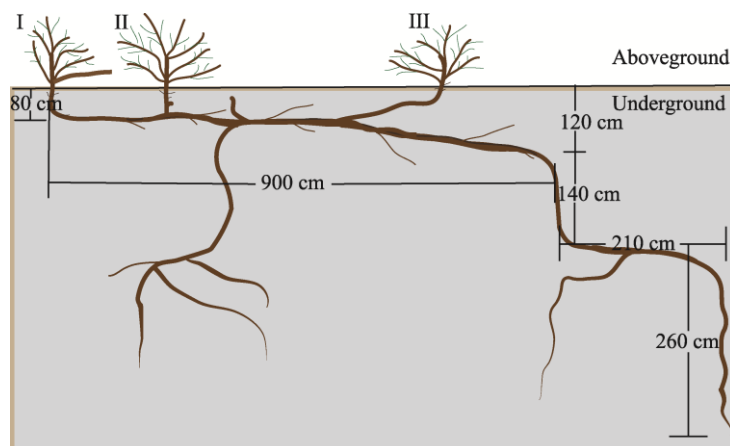


Fig. 7 Sketch of root distribution in the profiles of different *T. taklamakanensis* plants (I, II and III) in the same *T. taklamakanensis* nabkha

In the Qira site, the $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of plant xylem water were most similar to those of soil water below the soil depth of 480 cm (Fig. 5c). Moreover, the contribution of deep soil water to the xylem water of *T. taklamakanensis* plants accounted for a large proportion of water utilization, with the percentage of 35% ($\pm 1\%$), and the contributions of shallow and middle soil water and groundwater were 7% ($\pm 1\%$), 25% ($\pm 1\%$) and 33% ($\pm 1\%$), respectively (Fig. 6). In the Aral site, the $\delta^2\text{H}:\delta^{18}\text{O}$ ratios of plant xylem water were more enriched than those of groundwater, and they were most similar to those observed for soil water below the soil depth of 400 cm (Fig. 5d). The contribution of deep soil water 38% ($\pm 2\%$) constituted the largest percentage of xylem water of *T. taklamakanensis* plants. The contributions of shallow and middle soil water and groundwater were 9% ($\pm 2\%$), 22% ($\pm 1\%$) and 31% ($\pm 1\%$), respectively (Fig. 6). However, previous studies indicated that the groundwater depth in the Qira and Aral sites was 11.0–16.0 and 8.0–10.0 m, respectively (Fan et al., 2013; Zeng et al., 2013). Li et al. (2009) showed that *T. taklamakanensis* could not survive when the groundwater depth was more than 15.7 m. Furthermore, *T. taklamakanensis* nabkhas were relatively high in the Qira and Aral sites (Table 1). This suggested that deep soil water was the primary water source of *T. taklamakanensis* in the desert-oasis ecotone habitat, and that groundwater may also be an essential water source.

Since the groundwater depth was relatively deep in the Qira and Aral sites, we inferred that soil water cannot be completely recharged by groundwater. This result may be partially explained by the locations of the Qira and Aral sites, where the water resource demands have been continuously increasing such that the groundwater depth may be in decline. In addition, *T. taklamakanensis* nabkhas were higher in the Qira site than in the Aral site, and the groundwater depth in the Qira site was deeper than that in the Aral site. This also partly explained why *T. taklamakanensis* can absorb soil water below the depth of 480 cm in the Qira site while absorb soil water below the depth of 400 cm in the Aral site. These findings confirmed that *T. taklamakanensis* can tolerate the arid environment. Furthermore, these results supported our hypothesis that *T. taklamakanensis* utilizes the middle and deep soil water and/or groundwater, and demonstrated that the roots of *T. taklamakanensis* in the surface soil layer may be inactive because of the low SWC. This inactivation seems to be an adaptive choice of plants under dry and water-deficient conditions in the desert environment.

3.5 Implication of *T. taklamakanensis* nabkhas

Groundwater and deep soil water were the dominant water sources for the survival of plants in the Taklimakan Desert, where the groundwater depth ranged from 3.0 to 15.0 m (Zeng et al., 2013). Most *T. taklamakanensis* nabkhas were primarily distributed within the fringe regions of the

Taklimakan Desert, and the height and length of these nabkhas ranged from 3.00 to 15.00 m and from 5.00 to 50.00 m (long axis), respectively (Muhtar et al., 2002). In the study sites, the average height and length of *T. taklamakanensis* nabkhas were about 3.00 and 7.00 m, respectively. *T. taklamakanensis* can grow on the high sand dunes and primarily utilize deep soil water and groundwater to maintain their survival and meet their growth needs. Nevertheless, as the height of *T. taklamakanensis* nabkhas increased (above 15.00 m) and the groundwater depth dropped to below the extent of the roots, *T. taklamakanensis* nabkhas may begin degenerating and *T. taklamakanensis* plants may die, which will intensify the desertification (Xia et al., 2004). Groundwater depth did not limit their survival and growth in this study. Therefore, *T. taklamakanensis* nabkhas may reflect the changes in the groundwater depth and may also act as indicators of environmental change in the desert environment.

Horton and Clark (2001) showed that *T. taklamakanensis* may not only obtain groundwater through the deep roots but also can acquire water from the unsaturated areas of soil (Cleverly et al., 2002). Gries et al. (2003) indicated that *T. taklamakanensis* was established by the germination of plant seed in the lowland zones and can also be established through clonal growth in the crests and slopes of the sand dunes (Muhtar et al., 2002). During the field sampling, we found that *T. taklamakanensis* was established through clonal growth, and its taproots extended horizontally by a certain distance and then gradually extended downward (Fig. 7). Furthermore, we found that in the same *T. taklamakanensis* nabkha, several *T. taklamakanensis* plants within a certain distance shared the same taproot system (Fig. 7). These results also confirmed the reasons for the capability of *T. taklamakanensis* to grow on the high sand dunes.

4 Conclusions

In this study, we used the stable isotope analysis to investigate the water use strategies of *T. taklamakanensis* growing on the *T. taklamakanensis* nabkhas in the different habitats. In the Taklimakan Desert, groundwater was recharged by the river runoff from snowmelt water in nearby mountain ranges. *T. taklamakanensis* growing in the different habitats had different water use strategies and they can change their water use patterns according to the climate characteristics, size of *T. taklamakanensis* nabkha, groundwater depth, plant cover and soil texture. In the sandy desert habitat, where the surface SWC was depleted, *T. taklamakanensis* primarily utilized the middle and deep soil water and groundwater. In the saline desert-alluvial plain habitat, where the SWC increased with soil depth, *T. taklamakanensis* mainly utilized the deep soil water and following the groundwater. In the desert-oasis ecotone, *T. taklamakanensis* primarily utilized the deep soil water and may also use groundwater. Thus, the potential water sources of *T. taklamakanensis* were largely dependent on the groundwater depth and specific habitats. The water use strategies of *T. taklamakanensis* mirrored its adaptation to different habitats in the desert ecosystem.

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